

**SAV Bed Architecture: Water Depth Distribution and Cover
of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria
americana***

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1. Introduction

The St. Johns River is a 500 km long, north-flowing, blackwater river located within the upper eastern extent of peninsular Florida, USA. The lower 131 km of the St. Johns River includes the St. Johns estuary and a tidal, freshwater reach which, collectively, are called the Lower St. Johns River (LSJR). The LSJR begins just north of Little Lake George and flows north through the city of Jacksonville where it turns eastward and empties into the Atlantic Ocean at Mayport, Florida. (Fig.1). Along the shores of the predominantly broad (5 km) and shallow (< 4 m) LSJR are hundreds of kilometers of potential littoral shelves (water depth < 1 m), many of which are populated by meadows of submerged aquatic vegetation (SAV) (Bartram, 1773; DeMort, 1991; Sagan, 2003a).

Ten species of freshwater and brackish angiosperms as well as two charophyte genera are routinely seen along the littoral shelves of the LSJR during field surveys. An analysis of field data collected from 1998 through 2003 found *Vallisneria americana* Michx. was the dominant species basin-wide (Sagan 2003a). *V. americana* appeared on 84% of the transects with SAV. It accounted for 66.7% of the total SAV cover. Two other dominant species included *Najas guadalupensis* (spreng.) Magnus and *Ruppia maritima* L. They accounted for 16.4% and 8.3%, respectively, of total cover. *R. maritima* was notable because it was the only halophyte present within the river.

SAV habitat is crucial to the maintenance of a balanced ecosystem, providing refuge, food, habitat, and nursery sites for an assemblage of aquatic organisms including the endangered West Indian manatee (*Trichechus manatus*) (White et al., 2002). Many of these organisms, such as largemouth bass, catfish and blue crab are of substantial

recreational and commercial value within the LSJR (Watkins, 1995).

However, many stressors to SAV exist in the LSJR ecosystem. Light attenuation is thought to be an important factor limiting SAV distribution and abundance throughout the LSJR. High color, epiphytic and planktonic algae blooms, and suspended solids, increase the level of light attenuation within the water column and often characterize the LSJR. An additional stressor to SAV was seen during 1999 – 2001, when drought-induced increases in salinity had deleterious effects on the SAV in the lower reach of the river (Sagan 2003a).

Many of these stressors limiting SAV distribution are anthropogenic in origin, and therefore potentially manageable. It would be useful to obtain maximum water depth distribution of dominant species at current light attenuation thresholds in order to establish habitat requirements for SAV. The objective of this paper was to determine if there were differences in the depth distribution between the three dominant SAV species and whether distribution varied according to season. In addition, within-bed distribution (bed architecture) of these species was obtained.

2. Materials and Methods

2.1 Monitoring Sites and Data Collection Frequency

Since fall 2000, four years of seasonal SAV data were collected at seven permanent monitoring sites within the LSJRB (Figure 2). The seven sites include, in decreasing latitudinal order, Bolles School (BOL), Buckman (BUC), Moccasin Slough (MOC), Doctors Lake (DRL), Scratch Ankle (SCA), Rice Creek (RIC), and Crescent Lake (CRL). BOL, BUC, and MOC were located in the oligohaline – mesohaline section

of the river and were approximately thirty, thirty-five, and forty river miles, respectively, from the mouth of the SJR. SCA and RIC were located in the freshwater section and were approximately sixty and seventy-five river miles, respectively, from the mouth of the SJR. DRL and CRL were located in major water bodies flowing into the St. Johns River. DRL is located in Doctors Lake, an oligohaline lake flowing into the SJR just north of MOC. CRL is located in Crescent Lake, a freshwater lake discharging into the SJR via Dunns Creek.

A summary of survey dates is included in Table 1. Four years of fall, winter, spring, and summer data were included from fall 2000 through summer 2004. The exception was MOC and CRL. For MOC, there were only three seasons of fall data available. At CRL, the site was devoid of SAV during 2003 spring, fall, and winter sampling. In addition, winter 2004 SAV was very sparse at this site and therefore no SAV was present along increments sampled. Therefore, only three seasons of spring and fall and only two seasons of winter sampling were available for CRL.

2.2. Methods

Data collection at each site was conducted according to the following methodology. Ten transects were placed perpendicular to the shore starting from the shoreline and were extended towards the river channel. Along five transects, positioned at a distance of 0, 12, 25, 38, or 50 m from a stationary benchmark, water depth was recorded at 1-m intervals. Along an additional five, randomly positioned transects, linear cover of all SAV species was recorded. Linear cover was obtained by recording the length of tape intercepted by each species and by bare ground along the entire length of

the SAV bed. Interception of the tape included both interception by the plant and aerial interception of SAV foliage perpendicular to the tape. For example, intercept length was recorded as follows: bare ground 0 – 4.50 m, *Najas guadalupensis* 4.50 – 6.05 m, *Ruppia maritima* 5.00 – 6.00 m, bare ground 6.05 – 8.40 m, *Vallisneria americana* 8.40 - 60.55 m. Sampling was not coordinated with tidal flow and therefore occurs across all tide regimes. Diurnal tidal ranges (the difference in height between mean higher high water and mean lower low water) throughout the sampling area vary from 0.90 ft to 1.39 ft. These ranges were obtained from the verified historic NOAA database.

2.2. Data Analysis

For this analysis, water depth and linear cover data corresponding to 5-m increments were extracted from the SAV database. Water depth data collected at 5-m intervals along the length of the bed were used for analysis. Linear cover data were calculated for *N. guadalupensis*, *R. maritima*, and *V. americana* from 1-m distances corresponding to 4.5 – 5.5 m, 9.5 – 10.5 m, 14.5 – 15.5 m, etc. along each transect, converted to percent median cover, and were used for analysis. With the exception of three increments at MOC, one-way ANOVA analysis of water depth at 5-m increments between transects for each site during the same season and year (season-year), found no significant differences between transects. Therefore, it was deemed valid to group water depth values at these increments to obtain a representative median for each increment, site, and season-year.

Data met assumptions of normality therefore, data from all transects and sites were combined to obtain a comparison of water depth between seasons using a

parametric one-way ANOVA. Those groupings found to be significant ($p < 0.05$) were then tested with the Scheffes test to determine which seasons were significantly different.

In order to compare maximum water depth for each species, the median maximum water depth at each site for each season-year sampling event was calculated for each species. These values were used in a parametric one-way ANOVAs to investigate 1) inter-seasonal differences in maximum water depth distribution for *N. guadalupensis*, *R. maritima*, and *V. americana* and 2) year-round interspecific maximum water depth distribution. Those groupings found to be significant ($p < 0.05$) were then tested with the Scheffes test to determine which seasons were significantly different.

For each site and season, median percent linear cover at each 5-m increment was calculated for each species along with median water depth. A water depth distribution range for each species was also obtained. The statistical package used for all analyses was Statview (SAS Institute, Inc., 1999).

3. Results

As shown in Table 1, winter, spring, summer, and fall seasons were identified as occurring during the months of January – March, April – June, July – September and October – December, respectively. Whenever possible, data collection was concentrated during the months of February, May, August, and November. Significant differences ($p < 0.0001$) in water depth were found between seasons as follows: Fall > Sum > Spr = Win (Fig. 3). Mean water depths ranged from $0.67 \text{ m} \pm 0.25$ (mean \pm STD) in the fall to approximately $0.51 \text{ m} \pm 0.23$ in the winter and spring.

V. americana and *N. guadalupensis* maximum water depth distribution followed a similar pattern (Figs. 4 and 5). Fall maximum water depth ($0.87 \text{ m} \pm 0.20$) for *V. americana* was significantly greater than both spring and winter depths ($0.70 \text{ m} \pm 0.20$, $p=0.0143$ and $0.70 \text{ m} \pm 0.17$, $p=0.0118$, respectively). Fall maximum water depth ($0.83 \text{ m} \pm 0.25$) for *N. guadalupensis* was significantly greater than spring ($0.60 \text{ m} \pm 0.24$, $p=0.0305$) and significantly greater than winter at $p<0.1$ ($0.60 \text{ m} \pm 0.19$, $p=0.0504$). Maximum water depths during the summer were not significantly different from any other season for either species. No differences in maximum water depth were found between any seasons for *R. maritima* (Fig. 6).

Interspecific comparisons of maximum water depth distribution showed significant differences between all species (Fig. 7). Year-round maximum water depth for *V. americana* ($0.77 \text{ m} \pm 0.20$) was significantly greater than that of *N. guadalupensis* and *R. maritima* ($0.68 \text{ m} \pm 0.24$, $p=0.0204$ and $0.53 \text{ m} \pm 0.21$, $p<0.0001$, respectively). Fall maximum water depth for *Najas guadalupensis* was significantly greater than that of *R. maritima* ($p=0.0003$).

Distribution of the SAV species throughout the bed and across seasons shows some general trends (Figs. 8 - 14). *V. americana* was distributed throughout the bed, occurring in mixed near-shore zones along with *N. guadalupensis* and *R. maritima*, often at 100% cover, while it dominated the outer and deep-water sections of the bed. *N. guadalupensis* had the next greatest distribution, often co-occurring with *V. americana* but often at a much reduced percent cover. *R. maritima* had the most restricted distribution, inhabiting the shallowest near-shore third to half of the bed and with cover

usually below 50%. The exception to this trend was *R. maritima* distribution at BOL (Fig. 8) where its distribution mirrored that of *N. guadalupensis*.

Seasonal changes of distribution for *V. americana* were subtle. While at most sites (Figs. 8 - 14) incremental occurrence of *V. americana* and cover (=100%) were greatest during the summer, differences between seasons were not stark. *N. guadalupensis* also showed great variability between sites. *R. maritima* was only present in any great frequency at BOL, BUC, & MOC.

More conspicuous was the latitudinal distribution of *R. maritima*. This species had the greatest cover and bed-wide distribution at BOL. Both cover and distribution decreased with each upstream site until *R. maritima* was only marginally present at RIC and not present at all at CRL.

4. Discussion

Investigating seasonal differences in SAV distribution is useful for a variety of reasons. This is an important feature of seasonality that should be considered before grouping yearlong survey data together and comparing sites or yearly data. Like most systems, water quality parameters follow seasonal patterns which shape SAV growth and distribution into distinct temporal patterns. These seasonal differences may be exacerbated by unusual hydrologic or weather phenomena, such as the drought of 1999 – 2001. During that period increases in salinity in the downstream region of the LSJR caused decreases in distribution, diversity, and abundance of SAV. Further upstream at CRL, decreases in color, and presumably light attenuation, caused significant increases in SAV abundance (Sagan 2002).

Identifying seasonal changes is instructive in terms of identifying a growing season for LSJR SAV. It is also important for identifying seasons in which stressors are at a maximum so management decisions may be made to lessen any anthropogenic impact on SAV habitat. For instance, in the Caloosahatchee Estuary, resource managers are attempting to identify the time of year and flow volume in which freshwater discharge into the estuary would have the least deleterious effect on SAV (Doering et al. 1999, Doering et al. 2001). Similarly, proposals to withdraw drinking water from the SJR should consider seasonal stressors. The seasonal changes in the LSJR elucidated here may be explained as follows.

One of the environmental variables potentially affecting SAV distribution is water depth. Water depth was found to be higher in the fall which is not surprising given the orientation of the mouth of the river relative to winds originating from the northeast. High velocity northeasters increase oceanic water volume at the mouth of the river, impeding downstream river flow. This causes higher river volumes as well as higher high tides. In the winter and spring, winds are of southeast origin. Downstream flow, therefore, is not impeded by oceanic volume at the river's mouth. This results in lower water volume as well as lower seasonal tides.

Another variable affecting SAV distribution is light attenuation. Light attenuation coefficients values (K_d) in the LSJR ranged from 0.84 m^{-1} to 9.35 m^{-1} . K_d values were generated with an optical properties model which uses turbidity, color, and Chl-a values obtained bi-weekly since fall of 1997 from each site (Smithsonian Institution, 2002). Color, which has been shown through this model to be the variable predominantly affecting K_d , ranged from 10 CPU to 1000 CPU.

Given that water is deepest in the fall and that color is highest in the fall and winter in the LSJR (Aldridge et al. 1998), it is counterintuitive that both *V. americana* and *N. guadalupensis* had the greatest water depth distribution in the fall when light attenuation would be highest. However, two explanations are plausible both of which assume SAV was not colonizing greater depths during the fall but was surviving within a deeper seasonal water column. SAV can morphologically and physiologically adapt to low light conditions. *V. americana* will counteract light attenuation by preferentially shunting resources towards leaf elongation (Blanch et al. 1998; Doyle and Smart 2001) and thereby concentrating plant foliage near the water surface where light irradiance levels are higher. During the fall, I have documented leaf elongation in *V. americana* (Sagan 2004) and have observed *N. guadalupensis* plants that, much like *Hydrilla sp.* (Steward 1991; Van et al. 1999), concentrates biomass towards canopy production resulting in a floating mat of leaves and stems suspended from a single, rooted vertical stem. In addition, *V. americana* was found to increase total chlorophyll production in response to increased light attenuation (Barko and Filbin 1983)

Another explanation is that below-ground reserves, accumulated during the spring and summer when irradiance is high and/or water column depth low (Blanch et al. 1998), sustain the plants during the fall as light availability declines through a lengthening (and darkening) water column. Lower winter maximum water depths at which *V. americana* and *N. guadalupensis* were found may be an indication that plants at the deepest part of the bed died once reserves ran out. Indeed, in most cases SAV bed lengths (i.e. distance from shore) were less in the winter than in the summer or fall. Lower depths during the spring may indicate that SAV had not yet recolonized those depths by vegetative

expansion. Although Dawes and Lawrence (1989) did not find seasonal resource allocation to stolons in *V. americana*, their study site was in a spring fed river in Central Florida. Neither seasonal changes in temperature nor water quality-induced changes to light attenuation occur in that river to the extent they do in the LSJR; thus important seasonal cues were missing that may, in the LSJR, activate resource allocation.

It was not surprising that *V. americana* had the greatest maximum water depth of all three species. *V. americana* is physiologically adapted to survive in low light conditions (Titus and Adams 1979; Korschgen and Green. 1988, Harley and Findlay 1994). It has been estimated that *V. americana* in the LSJR requires between only 2% to 8% of surface irradiance (Dobberfuhl 2004). It is routinely associated with the deep-water edge of the SAV bed in the LSJR and is often present in monospecific stands under water quality conditions that appear not to support other species. For instance, at CRL, all species of SAV, including *Hydrilla verticillata* but excluding *V. americana*, disappeared from the water body in 2003 when mean color the preceding year in the lake reached above 500 CPU (Sagan, 2003b). In addition, data here (Fig. 14) shows disappearance of *N. guadalupensis* corresponding to the fall season. While no similar information on water depth distribution or light requirements could be found for *N. guadalupensis*, it clearly does not have the ability to survive at irradiance levels that can sustain *V. americana*.

R. maritima distribution and light requirements are well documented. *R. maritima* stands are most often found within high light habitats and limited to the shallowest sections of SAV beds and to quiescent waters (Orth and Moore 1988; Duarte 1991; Kantraud 1991). In addition, Evans et al. (1986) found that photosynthesis of *R. maritima* was maximal at higher temperatures which gave it a competitive advantage over *Zostera*

marina in the shallowest part of the SAV bed. However, in the LSJR *V. americana* and *N. guadalupensis* co-occur with *R. maritima* in the near-shore section of the bed. Further, the cover of *R. maritima* rarely exceeds that of *V. americana*. However, *R. maritima*, a halophyte, does have a competitive advantage over the freshwater species, *N. guadalupensis*. At those sites (BOL) or during seasons such as spring at BUC (Fig. 9) in which salinity is high, *R. maritima* fills the shallow-bed niche usually reserved for *N. guadalupensis*.

It is important to note that *R. maritima* had the lowest maximum water depth distribution of all three species and was generally restricted to the near-shore portion of the bed. This finding was substantiated by annual surveys in the LSJR (Sagan 2003a) that during high salinity times *R. maritima* did not fill the *V. americana* niche. In other words, it did not achieve the same cover, depth, or latitudinal distribution that *V. americana* did when salinity was not a limiting variable to the growth of *V. americana*. Therefore, when management decisions are made regarding issues such as surface water removal or dredging, activities which may artificially increase salinity, *R. maritima* will not provide a replacement habitat for crabs, fish, or manatees. Further, as Brody (1994) suggested, it is unlikely that seagrasses would fill this salinity niche because temperature extremes in the LSJR would not support *Thalassia* or *Zostera* and light attenuation levels are too high for *Halodule*.

In addition to elucidating SAV niche habitats, bed architecture findings demonstrate that SAV (usually *V. americana*) at the maximum water depth generally had low cover. This section of the bed is characterized by sparse, and often small plants (blade length < 5 cm), and usually only one species was present (personal observation). It

may be more biologically relevant to assess maximum water depth distribution for each species where maximum cover (i.e. 100 % - 300% total linear cover) occurs because many studies have shown SAV complexity is a predictor of fish and invertebrate diversity and abundance. Nekton abundance was positively correlated with SAV biomass (Raposa and Oviatt, 2000). Wyda and coworkers (2002) found that fish communities found in *Zostera marina* beds with biomass and density of > 100 wet g m⁻² and 100 shoots m⁻², respectively, had significantly higher species diversity, abundance, and biomass as compared to beds of low complexity. Setting light attenuation values that correspond to a maximum depth, therefore, may not result in SAV habitat that supports other biota.

An analysis of seasonal and within-bed SAV distribution may prove indispensable in determining how water quality parameters shape SAV habitat. These analysis may be the first step in identifying site-specific seasonal stressors and a more defined growing season for LSJR SAV. Further, pairing of these finding with water quality data obtained from each site may be particularly useful for establishing SAV habitat requirements and long-term protection goals.

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Source of Unpublished Materials

Dobberfuhl, D.R. 2004. Estimating minimum light thresholds for submerged aquatic vegetation in the Lower St. Johns River, Florida. Oral Presentation from the Semiannual Meeting of the Southeastern Estuarine Research Society. Fort Pierce, Florida.

Table 1
Summary of Sampling Dates.

Season-Year	Sampling Dates
Fall 2000	11/13/00 – 12/15/00
Winter 2001	02/06/01 – 03/02/01
Spring 2001	05/04/01 – 06/08/01
Summer 2001	08/06/01 – 09/07/01
Fall 2001	11/09/01 – 12/20/01
Winter 2002	02/11/02 – 03/22/02
Spring 2002	05/02/02 – 06/02/02
Summer 2002	08/07/02 – 09/11/02
Fall 2002	11/02/02 – 12/19/02
Winter 2003	02/01/03 – 03/12/03
Spring 2003	04/04/03 – 06/05/03
Summer 2003	08/11/03 – 09/18/03
Fall 2003	10/24/03 – 11/25/03
Winter 2004	02/03/04 – 03/14/04
Spring 2004	05/01/04 – 05/30/04
Summer 2004	08/02/04 – 08/31/04

Fig. 1
Survey area. Lower St. Johns River Basin, Northeast Florida, USA.

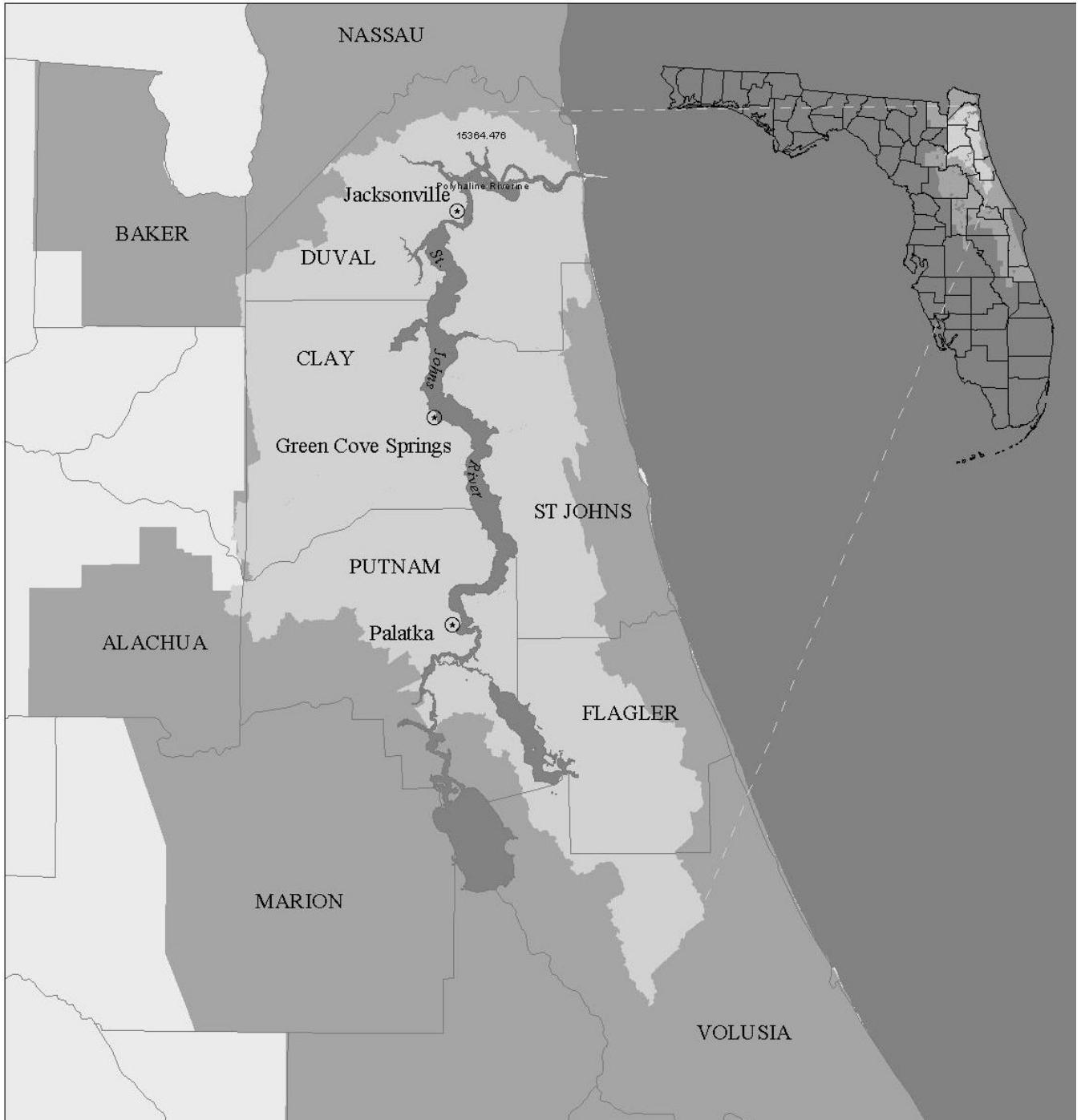
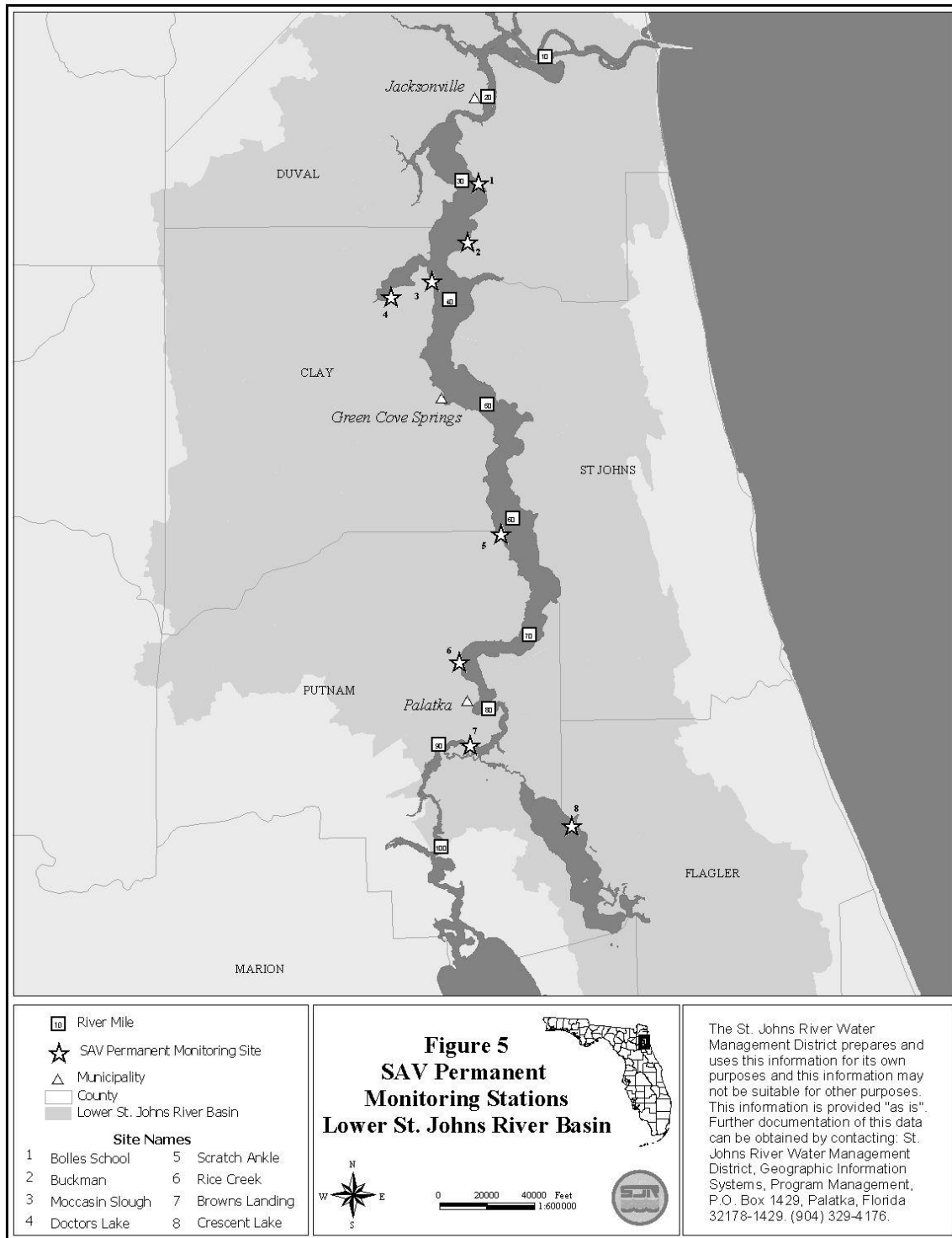
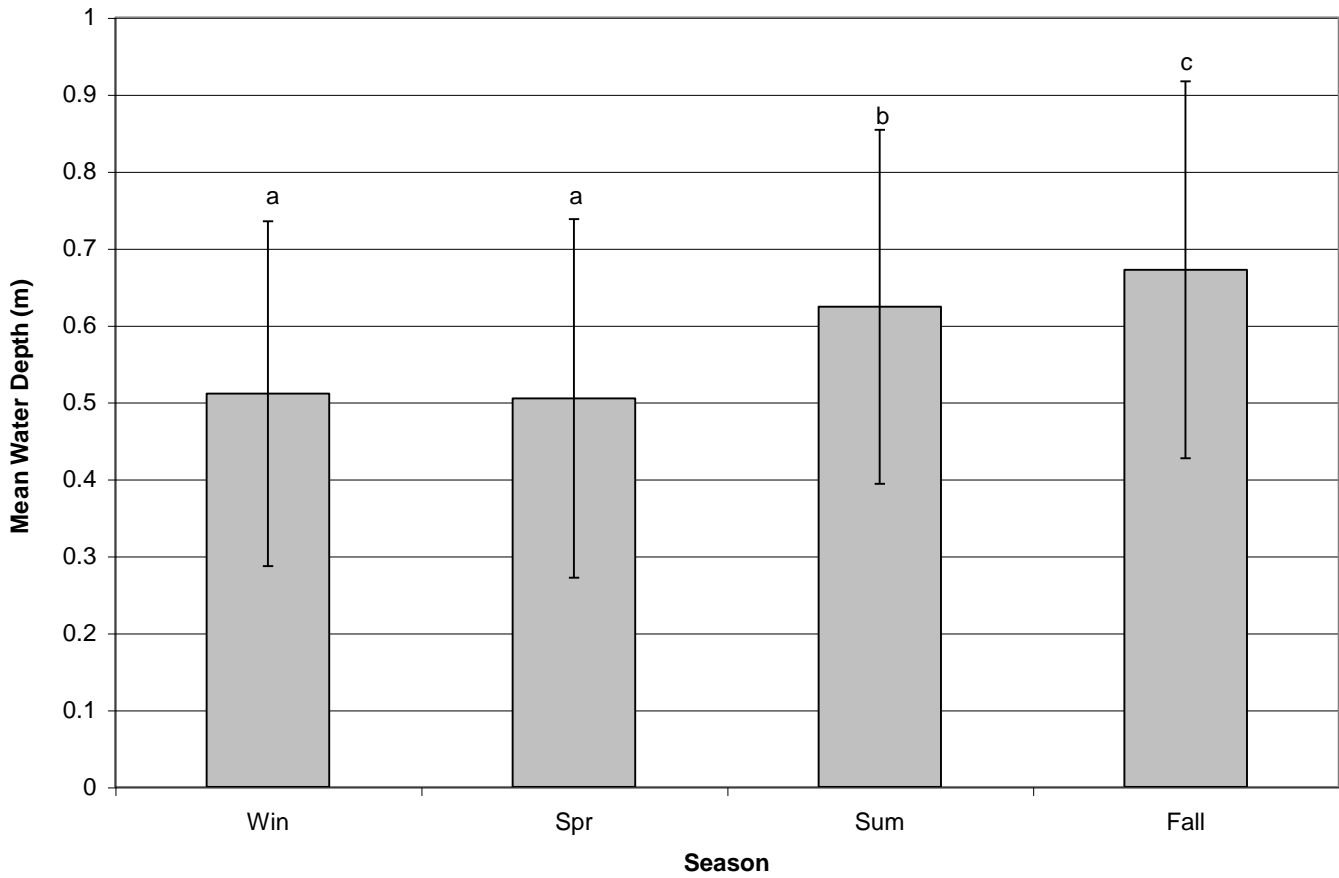


Fig. 2
 Location of permanent monitoring sites within the lower St. Johns River Basin.



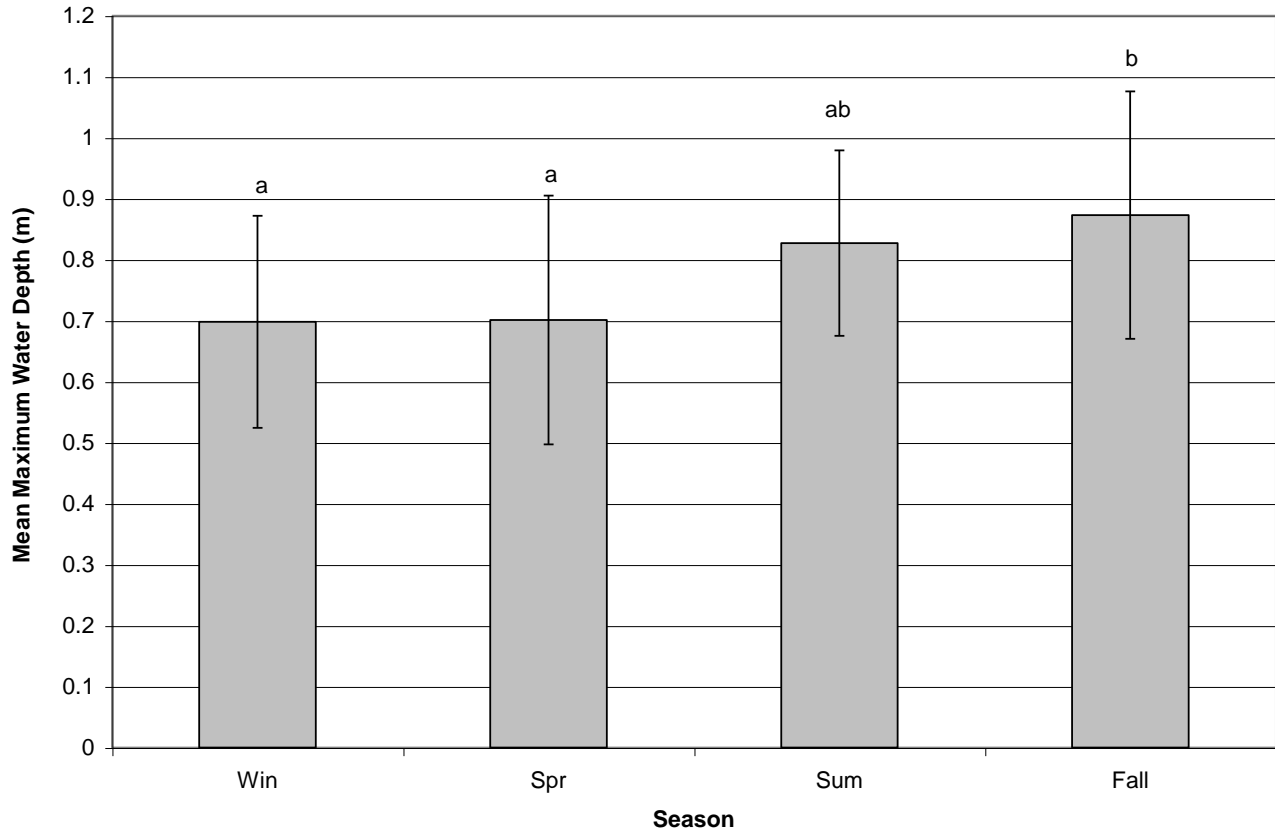
Source: v:\es4\gis_projects\sav\projects_pc\sav_2001_jsagan.apr 03/01/2002

Fig. 3
Seasonal Comparison of Water depth for Fall 2000 through Summer 2004



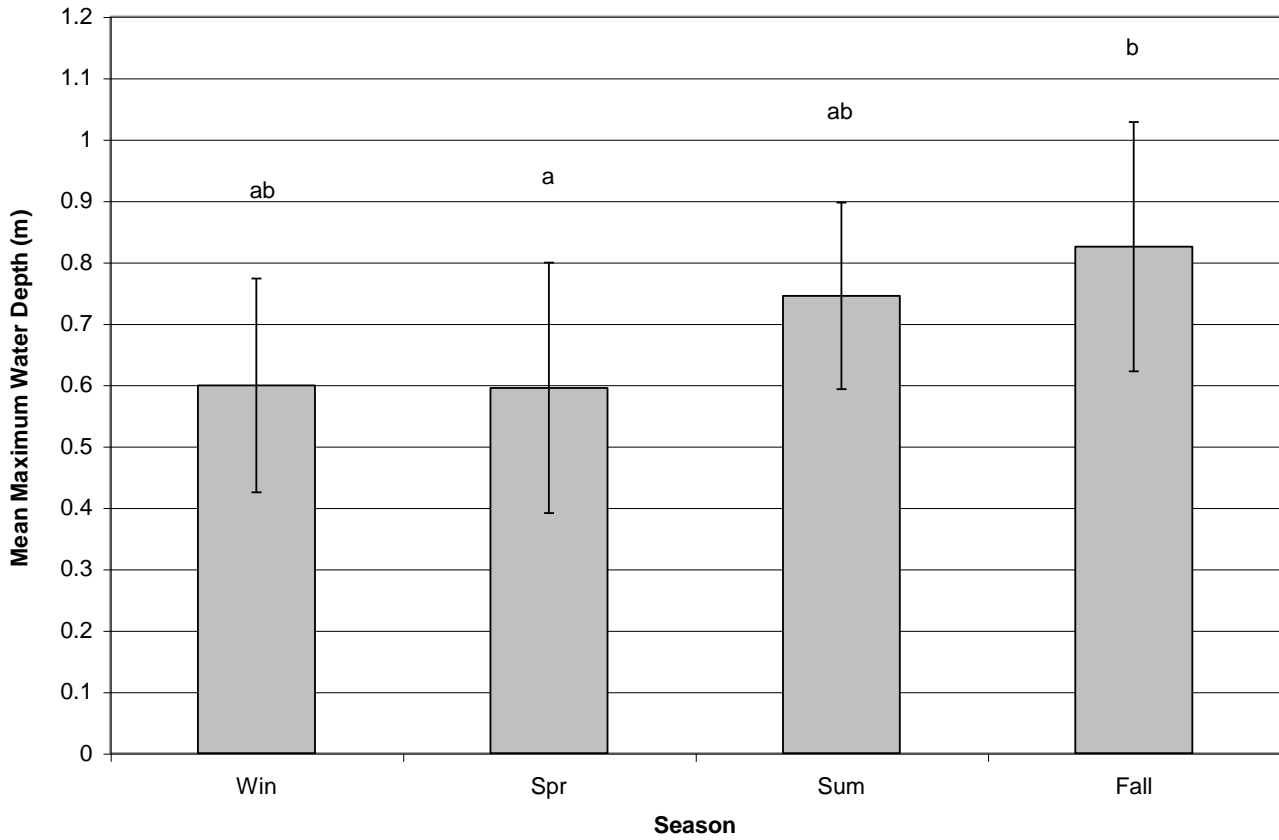
Values with different letters indicate a significant difference ($p < 0.0001$) between seasons. Data are mean \pm one standard deviation ($n = 2721 - 3213$).

Fig. 4
Seasonal Comparison of *Vallisneria americana* Maximum Water Depth Distribution for
Fall 2000 through Summer 2004.



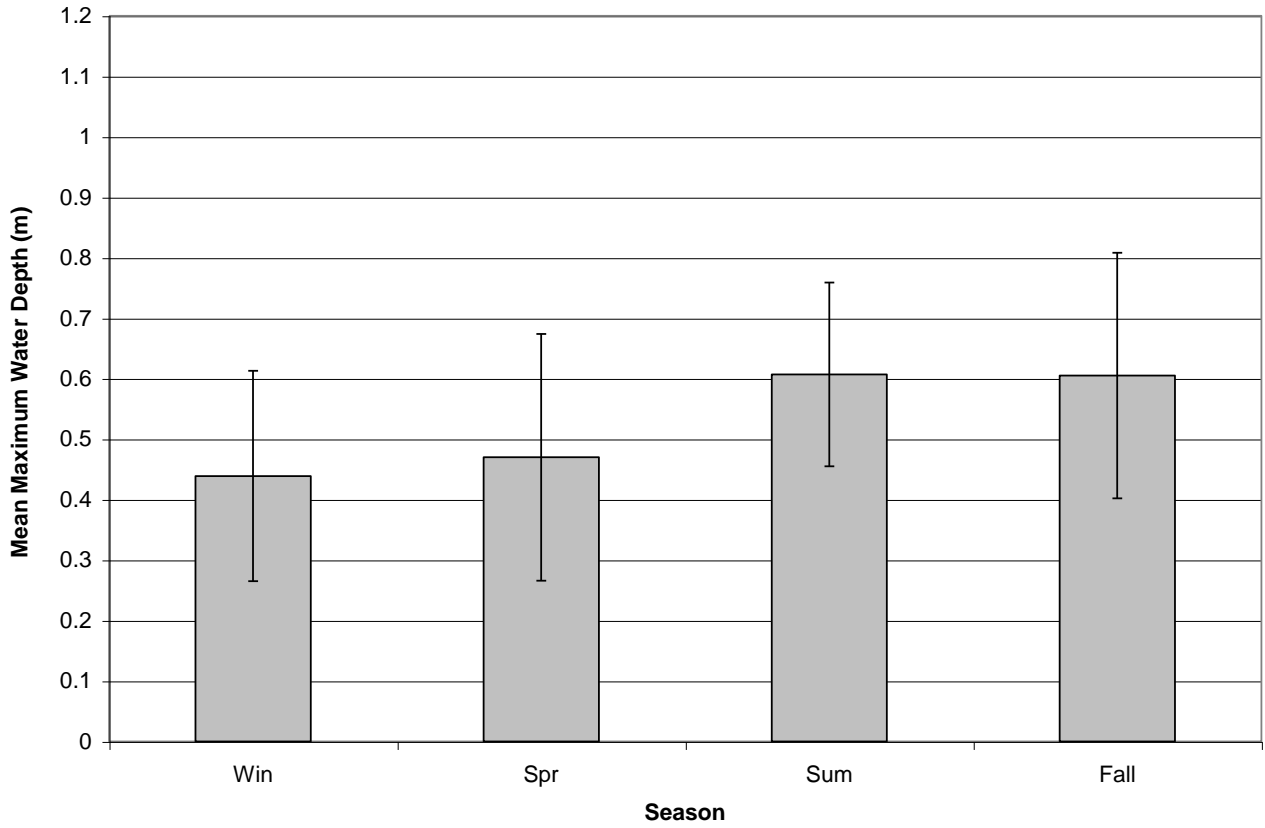
Values with different letters indicate a significant difference ($p < 0.001$) between seasons.
Data are mean \pm one standard deviation (n = 24 - 27).

Fig. 5
Seasonal Comparison of *Najas guadalupensis* Maximum Water Depth Distribution for Fall 2000 through Summer 2004.



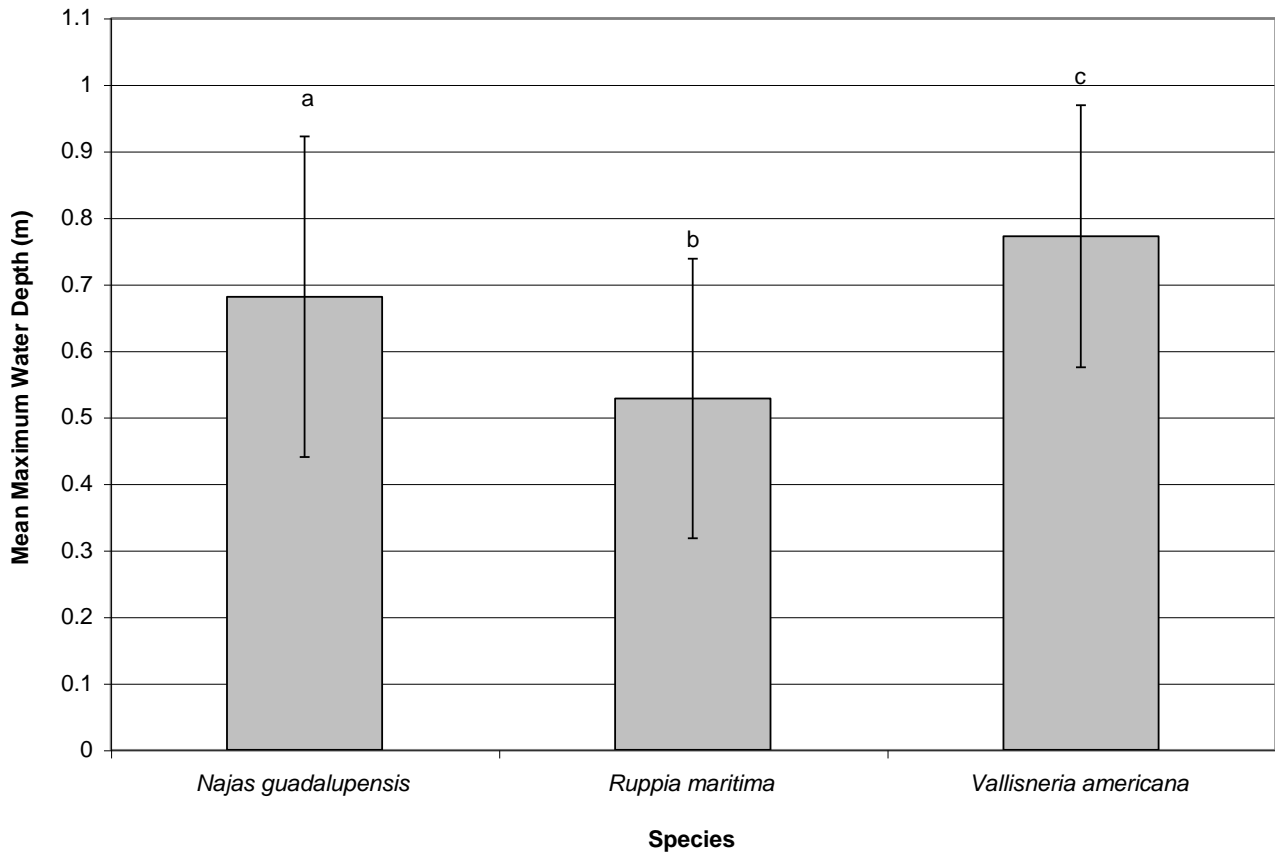
Values with different letters indicate a significant difference ($p < 0.05$) between seasons. Data are mean \pm one standard deviation ($n = 24 - 27$). Win and Fall values significantly different at $p < 0.1$ ($p = 0.0504$)

Fig. 6
Seasonal Comparison of *Ruppia maritima* Maximum Water Depth Distribution for Fall 2000 through Summer 2004.



Values with different letters indicate a significant difference ($p < 0.05$) between seasons. Data are mean \pm one standard deviation ($n = 13 - 17$).

Fig. 7
Interspecific Maximum Water Depth Distribution Across Seasons.



Values with different letters indicate a significant difference ($p < 0.01$) between species. Data are mean \pm one standard deviation (n = 57 - 105).

Fig. 8
 Water Depth Distribution of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*: Bolles School.

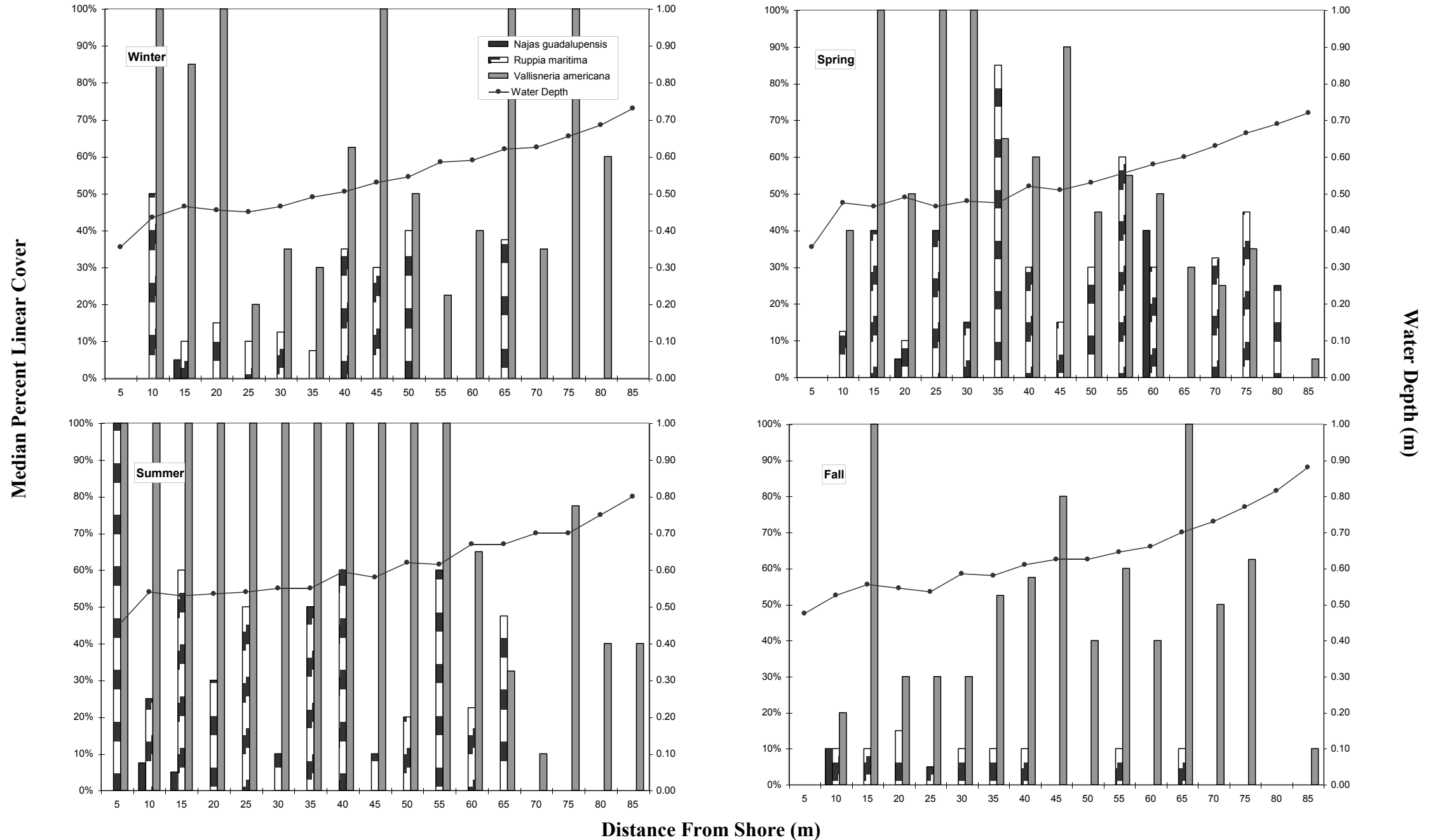


Fig. 9
 Water Depth Distribution of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*: Buckman.

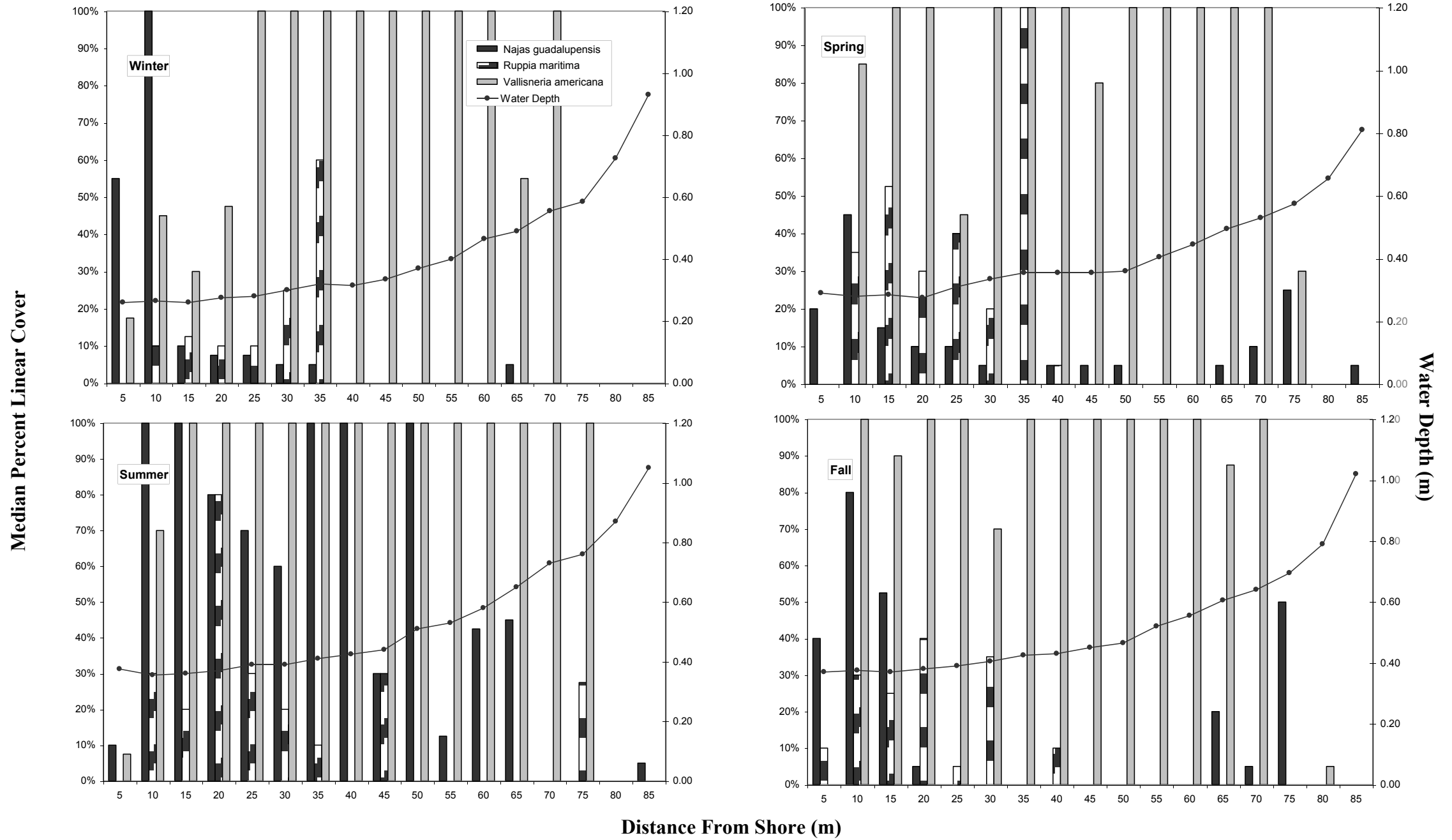


Fig. 10
 Water Depth Distribution of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*: Moccasin Slough.

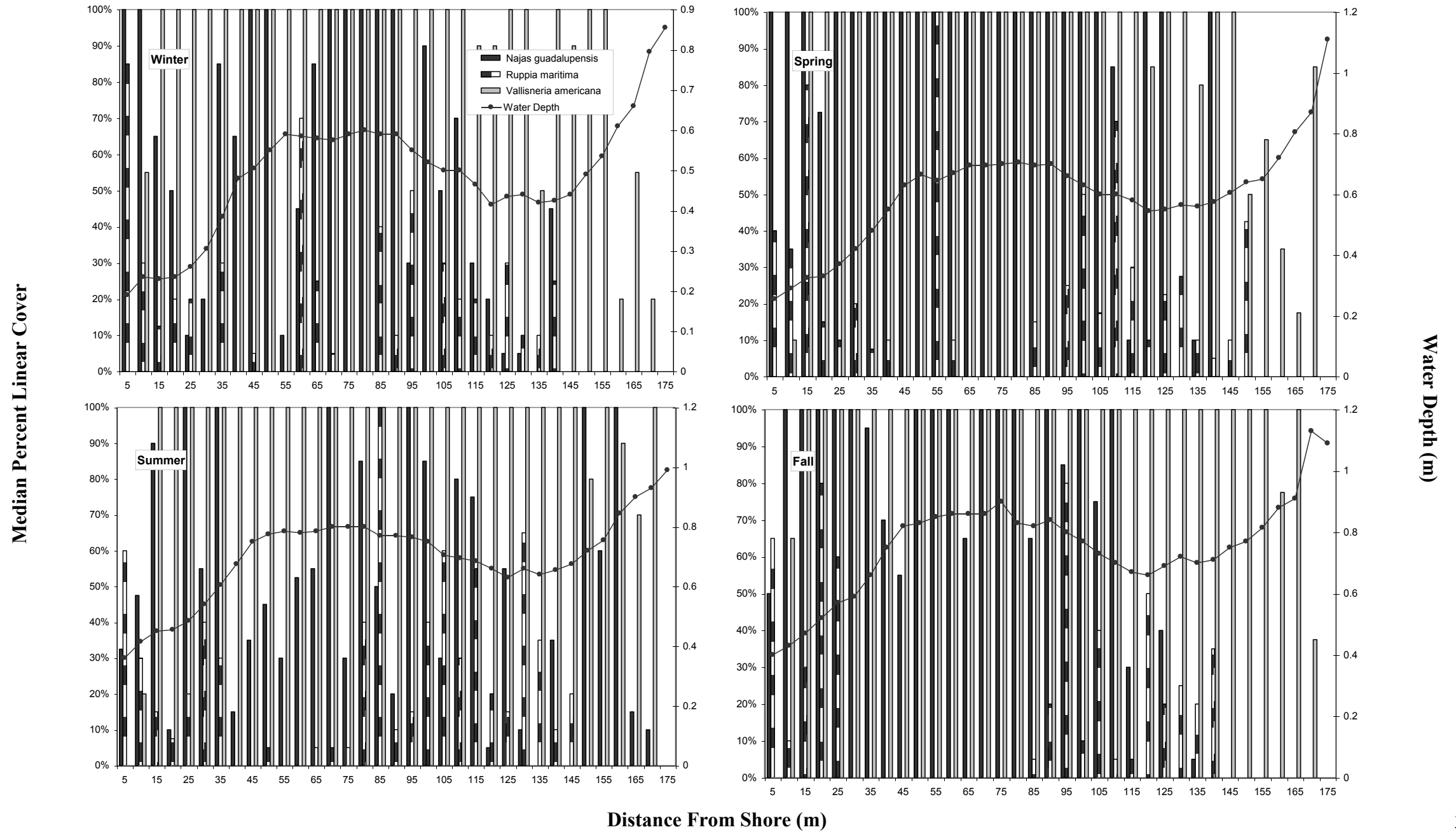


Fig. 11
 Water Depth Distribution of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*: Doctors Lake.

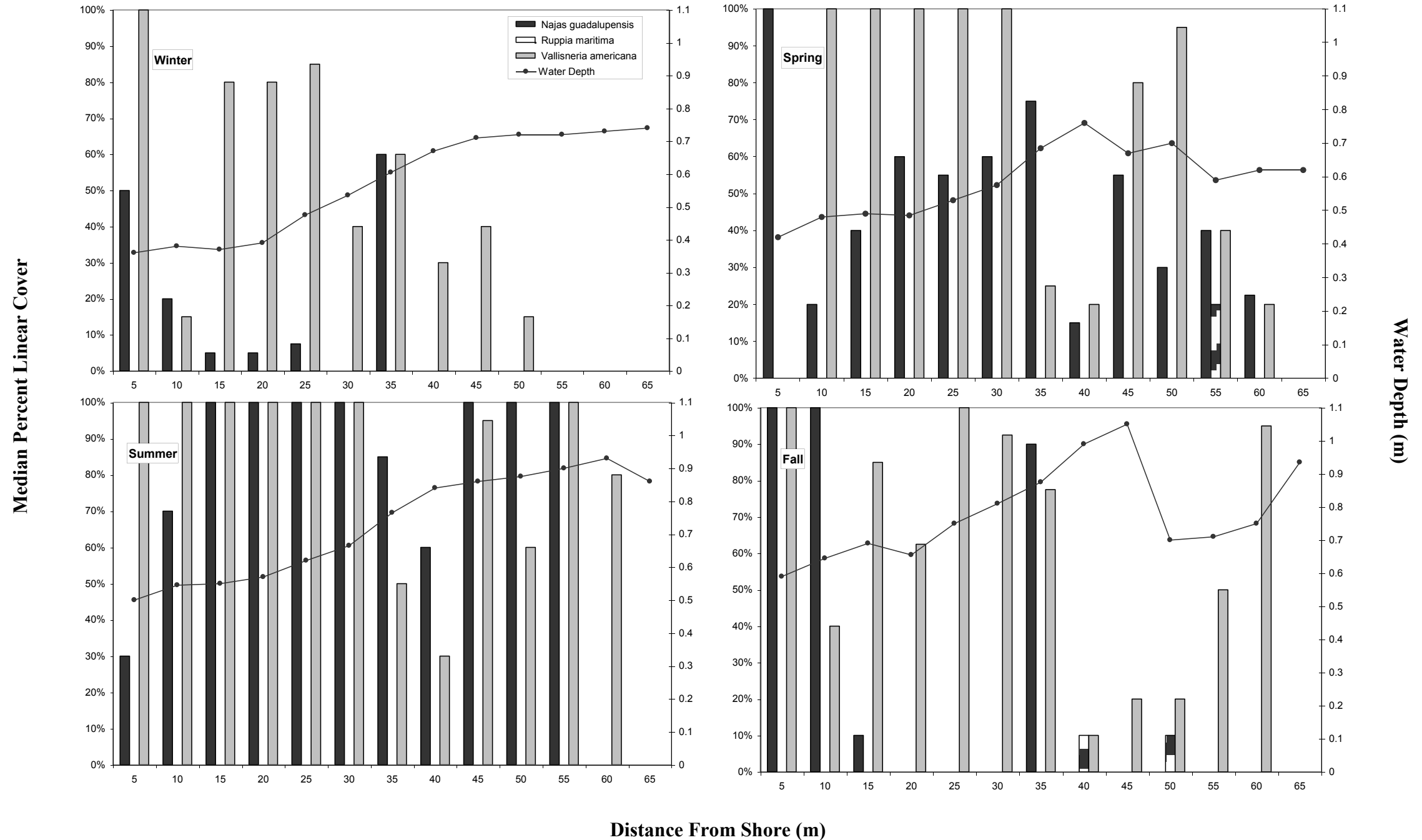


Fig. 12
 Water Depth Distribution of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*: Scratch Ankle.

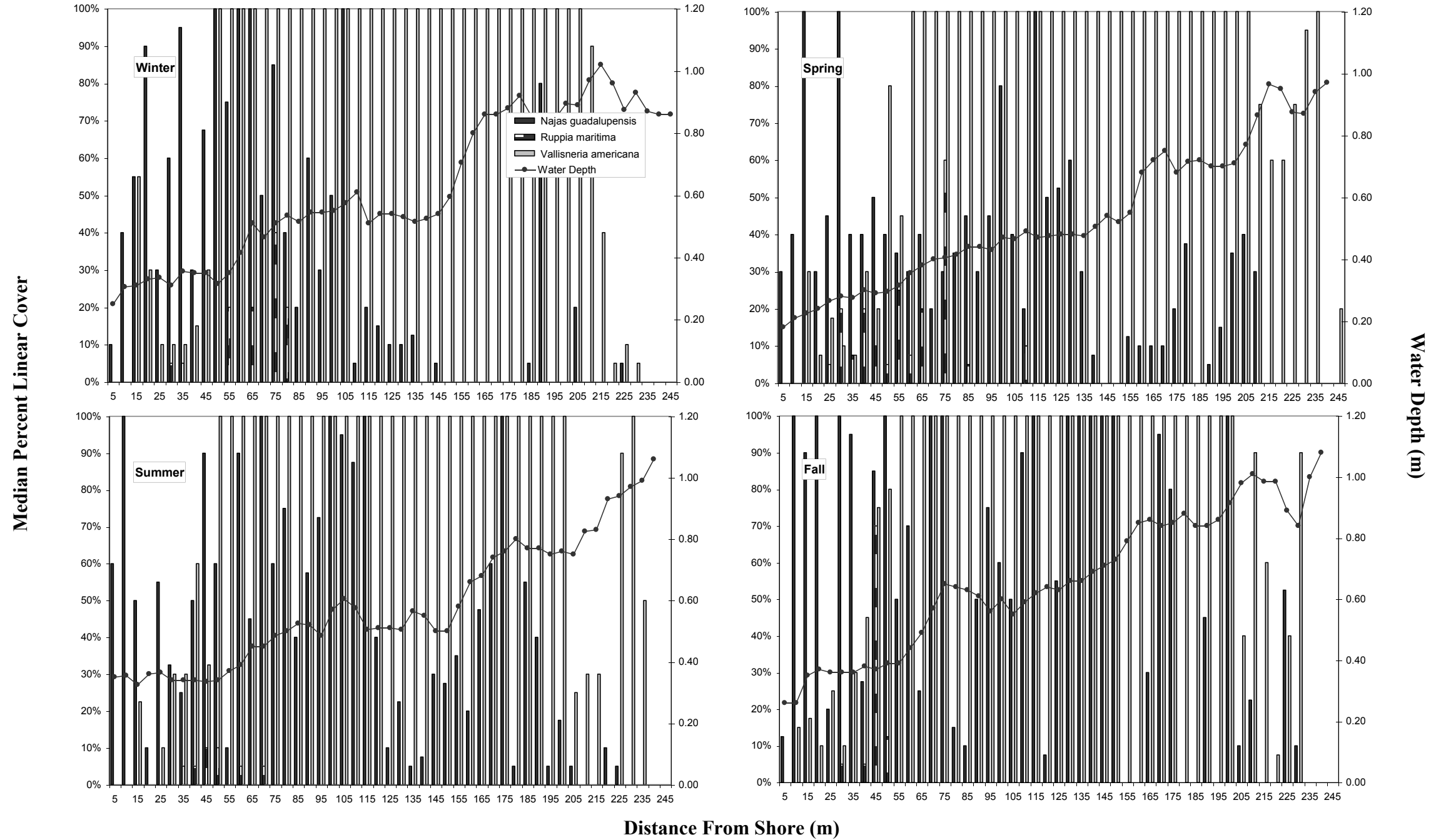


Fig. 13
 Water Depth Distribution of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*: Rice Creek.

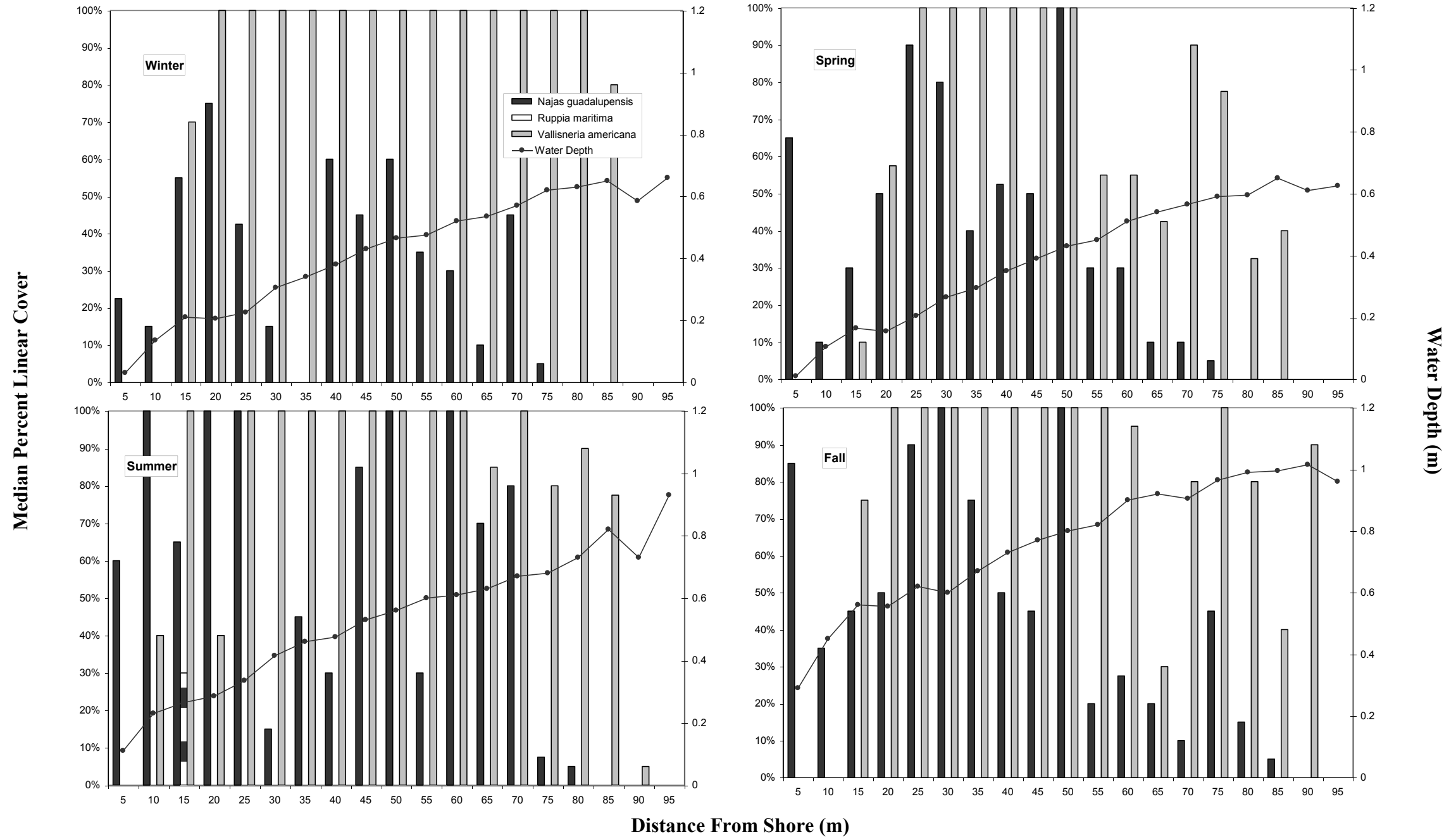


Fig. 14

Water Depth Distribution of *Najas guadalupensis*, *Ruppia maritima*, and *Vallisneria americana*: Crescent Lake.

